FLIGHT STRATEGIES OF MIGRATING OSPREY: FASTING VS. FORAGING

GRADY L. CANDLER[1] AND PATRICIA L. KENNEDY[2]
*Department of Fishery and Wildlife Biology, Colorado State University,
Fort Collins, CO 80523 U.S.A.*

ABSTRACT.—We developed energetics models to predict migration times and fat consumption rates of osprey (*Pandion haliaetus*) migrating south from their breeding grounds in the Intermountain West of North America. In these models we simulated three migration strategies: fasting, foraging at several mid-migration stopovers (jump strategy) and frequent foraging at stopovers (hop strategy). Because these piscivores appear to migrate predominantly over land and are rarely seen along ridges used by other migrant raptors that exploit deflection updrafts, we assumed they primarily used thermal soaring during migration. Our model predicts a 1.68-kg osprey would take 12 d and 0.25 kg of fat (a fat density of 15% of lean body mass), to complete a fasting migration of 3780 km (mean of migration distances estimated from 21 band recoveries of osprey nesting in northern Idaho and eastern Washington) when wind speed is 0 m s^{-1}. A sensitivity analysis of this model showed that changes in wind speed (± 5 m s^{-1}) had the greatest influence on migration time (8–21 d) and fat consumption (0.16–0.45 kg). In the foraging model, maximum fat deposition rate was predicted to be 0.04 kg d^{-1}. Given this prediction and assuming osprey settle for 1 d at each stopover, migrations with one, three (jump strategies), five or 11 (hop strategies) stopovers were predicted to take 17, 21, 25, or 34 d, respectively. With no settling time at stopovers the predicted foraging migration times only range from 15–17 d. The model predictions for both the foraging (without settling costs) and fasting migrations are consistent with the limited data available on fall migration strategies of osprey breeding in the Intermountain West. Our results also suggest that, under certain assumptions, nonstop migration may be energetically possible for western interior osprey.

KEY WORDS: *aerodynamic model; fat deposition; migration strategies; osprey;* Pandion haliaetus; *sensitivity analysis.*

Estrategias de vuelo de *Pandion haliaetus* migrantes; rapidez vs. forrajeo

RESUMEN.—Desarrollamos un modelo energético para predecir los tiempos de migración y tasas de consumo de grasas de *Pandion haliaetus* migrando hacia el sur desde sus áreas de reproducción en el oeste de Norteamérica. En estos modelos simulamos tres estrategias de migración: rapidez, forrajeo en varios sitios de descanso en el transcurso de la migración ("jump strategy") y forrajeo frecuente en sitios de descanso ("hop strategy"). Debido a que estas aves piscivoras parecen migrar predominantemente sobre el campo y raramente son observadas a lo largo de cordones montañosos, usados por otras rapaces migratorias que explotan la deflexión de corrientes de aire, presumimos que ellas se remontan usando corrientes de aire ascendentes. Nuestro modelo predice que un individuo de esta especie de 1.68 kg podría tomar 12 días y 0.25 kg de grasa en recorrer rapidamente 3780 km (distancia migratoria media, estimada de 21 individuos marcados), cuando la velocidad del viento es de 0 m/s. Un análisis de sensibilidad del modelo mostró que cambios en la velocidad del viento (± 5 m/s) tiene gran influencia sobre el tiempo de migración (ocho a 21 días) y sobre el consumo de grasa (0.16–0.45 kg). En el modelo de forrajeo, la tasa máxima de depositación de grasa, se estimó en 0.04 kg/día. Dada esta predicción y presumiendo que *P. haliaetus* se detiene un día en cada parada, se presume que migraciones con una, tres ("jump strategies"), cinco o once paradas ("hop strategies") toman 17, 21, 25 o 34 días, respectivamente. Sin establecerse en cada parada, el modelo de forrajeo predice tiempos de migración del rango de 15 a 17 días.

---

[1] Current address: New York Botanical Gardens, Bronx, NY 10458 U.S.A.
[2] PLK is the corresponding author.

Las predicciones del modelo tanto para la migración con forrajeo (sin costos de establecimiento) como para migraciones rápidas son consistentes con los limitados datos disponibles sobre las estrategias migracionales de otoño de *P. haliaetus* nidificantes en el oeste intermontañoso. Nuestros resultados sugieren que, bajo ciertas presunciones, la migración sin detenciones puede ser energéticamente posible para esta rapaz proveniente del oeste interior.

[Traducción de Ivan Lazo]

The migration strategies of long-distance migrants have been the focus of extensive research (see Baker 1982, Kerlinger 1989, Alerstam 1990 and Berthold 1993 for reviews), but it is still unclear whether many species of long-distance migrants make stopovers to feed during migration, rely totally on pre-migratory tissue deposition to fuel their migration, or use a combination of both strategies. Even the type of tissue accumulated for energy reserves during migration has come into question in recent years (fat vs. protein [Piersma 1990, Lindström and Piersma 1993]).

Using a bioenergetics model, Smith et al. (1986) predicted that the broad-winged hawk (*Buteo platypterus*) and the Swainson's hawk (*Buteo swainsoni*) could migrate from southern North America to northern South America (4300 km) without eating if they deposited fat amounting to 20–25% of lean body mass prior to migration. However, Smith et al. (1986) only evaluated one migration strategy (fasting). Similar to migration models developed for passerines and waders (Castro and Myers 1989, Gudmundsson et al. 1991, Lindström and Alerstam 1992), they did not conduct a sensitivity analysis of their model to evaluate the extent to which their model predictions vary with uncertainties in parameter values (see Kirkley 1991 and Goldstein and Smith 1991 for additional evaluations of the Smith et al. model).

Further insight could be provided on possible raptor migration strategies by creating models that compare fasting and foraging migration. However, the species modeled should be well-studied since empirical data are necessary for parameter estimation and for a preliminary evaluation of the realism of the model's predictions. In the United States, the osprey (*Pandion haliaetus*) is one of the few species of large raptors for which there are empirical data on its flight behavior (Kerlinger 1989), and migration distance and time (Henny and Van Velzer 1972, Melquist et al. 1978, Melquist and Johnson 1984, Poole and Agler 1987). Although there is an abundance of banding data on European osprey migrations (Österlöff 1977, Alerstam 1990), these migrations occur across large water barriers such as the Mediterranean and Baltic seas (Österlöff 1977, Alerstam 1990). These osprey use thermal

soaring over land but probably resort to flapping flight when crossing these water barriers (Kerlinger 1989, Alerstam 1990). Osprey breeding in the Intermountain West seem to migrate inland over the semi-arid southwestern United States and Central America (Henny and Van Velzer 1972, Melquist et al. 1978, Poole and Agler 1987) and probably use thermal soaring for the majority of their migration (Kerlinger 1989). We decided to model the migration strategies of osprey from the Intermountain West because the model would require fewer variables than a migration model of European osprey which would have to incorporate parameters (and assumptions) describing both thermal soaring and flapping flight.

In this paper we describe models that predict fall migration times and fat consumption rates for osprey breeding in the Intermountain West using three migration strategies: (1) fasting; (2) foraging at several mid-migration stopovers (jump strategy [Piersma 1987]); and (3) frequent foraging at stopovers (hop strategy [Piersma 1987]). We present results of a sensitivity analysis of the fasting model in which the parameter estimates were varied in a manner that reflects their empirical variation. This analysis provides insights into the key factors influencing model predictions and indicates the extent to which the model predictions vary with the uncertainties in the parameter estimates. A preliminary evaluation of the model is also presented in which we compare model predictions to empirical estimates of (1) osprey migration times from lookout observations and banding data and (2) raptor fat densities.

METHODS

Fasting Migration Model. To determine if these birds could deposit sufficient fat to fuel a fasting migration, an energetics model was constructed based on morphometrics, flight characteristics, diurnal activity patterns, energy cost of soaring flight, energy cost of roosting, and wind speed. This model assumes that fat deposits are the main source of energy during migration since there are no data available to estimate the role of other fuel resources used by osprey during migration. Values used as input parameters are shown as nominal values in Table 1. We assumed a migration distance of 3780 km. This distance is the mean of migration distances estimated from 21 band recoveries of osprey nesting in north-

ern Idaho and eastern Washington (Melquist et al. 1978, Melquist and Johnson 1984, Johnson and Melquist 1991).

Morphometric values were based on average measurements of body mass, wing span and wing area for osprey breeding in New York (Kerlinger 1989) because no comparable data sets were available for western osprey. Average mass (1.67 kg) of 33 adult osprey breeding in central Idaho (M. Bechard unpubl. data) is similar to the New York average (1.68 kg, Table 1), indicating the morphometric data on eastern osprey are a good approximation of western osprey morphometrics.

Using radar, Kerlinger (1989) measured the flight altitude of osprey using thermal soaring to migrate across central New York ($\bar{x}$ = 880 m). In our model the nominal value for flight altitude was 2000 m to compensate for the increased elevation of the western migration route. Since it is difficult to determine wind velocity and direction at migration altitudes, a nominal wind speed of 0 m s^{-1} was used.

The energy cost of soaring flight and cross-country velocity were estimated with a modification of Pennycuick's model (Program 2; 1989) which is derived from theoretical aerodynamics. We chose Pennycuick's model as the template for our model because it provides the most realistic estimates of migration flight costs in comparison with other aerodynamic models (Welham 1994). Output from Pennycuick's model predicts the amount of daily fat utilized, average cross-country velocity, and daily distance flown at the predicted velocity. This model uses climb rate as an input variable for determining cross-country velocity. A climb rate of 3 m s^{-1} was chosen for these calculations, based on Kerlinger's (1989) radar-tracking results of osprey migrating in New York. This may be a conservative estimate of climb rate since thermal updrafts in the Intermountain West are exceptionally strong (Hoffman 1985). Pennycuick's model also calculates basal metabolic rate (BMR) using Lasiewski and Dawson's (1967) allometric equation for nonpasserines and then uses this estimate in the flight-cost calculations. The accuracy of allometric equations for predicting BMR of falconiformes has been questioned by several investigators (Wasser 1986, Kennedy and Gessaman 1991). Therefore, we replaced the predicted BMR in Pennycuick's model with an active phase resting metabolic rate (RMR$_a$) based on energetics measurements of osprey. We estimated RMR$_a$ to be 1.24 × RMR$_r$ where RMR$_r$ is the mean resting metabolic rate (3.69 W kg^{-1}) of three captive osprey from Florida (Wasser 1986). We increased RMR$_r$ by 24% because active-phase measurements (RMR$_a$) average 24% higher than resting-phase (RMR$_r$) measurements in other raptors (Kennedy and Gessaman 1991).

Pennycuick's model uses these inputs of morphometrics and flight characteristics to calculate glide superpolar (GSP [dimensionless]), which describes the relationship between gliding sink speed and air speed, and interthermal velocity (V$_{it}$ [m s^{-1}]). V$_{it}$ is the velocity the osprey travels gliding between thermals. Pennycuick's model provides two estimates of V$_{it}$; V$_{opt}$ (m s^{-1}) and V$_{bg}$ (m s^{-1}). V$_{opt}$ is optimal interthermal speed which maximizes distance traveled per unit time, and V$_{bg}$ is a slower interthermal speed which maximizes glide distance. Interthermal velocities of osprey migrating in central New York (Kerlinger 1989) suggest they use an interthermal speed approximately 1-2 m s^{-1} less than V$_{opt}$. This would allow them to migrate faster than if they chose V$_{bg}$, while

still allowing them to glide farther and take advantage of stronger thermals than if they chose V$_{opt}$. Therefore, cross-country air speed of the osprey [V$_{xc}$, (m s^{-1})] was calculated using an interthermal velocity that was 2 m s^{-1} less than V$_{opt}$ estimated by Pennycuick's model.

Daily distance traveled (DDT [km d^{-1}]) was calculated as:

$$DDT = V_{xc} \times T_f \times (.001 \text{ km m}^{-1}),$$

where T$_f$ is daily flight time in sec. Daily fat consumed in flight (FFC [kg d^{-1}]) was calculated as:

$$FFC = (2RMR_a \times T_f)/ e,$$

where RMR$_a$ is in Watts and e is the energy content of fat (3.96 × 10^7 J kg^{-1} [Robbins 1993]). Although energetic costs are usually calculated from lean body mass because fat is relatively inert metabolically (Luke and Schoeller 1992), stored fat was included in these calculations of RMR$_a$ to account for the cost of increased wing loading due to pre-migratory fat deposits. The amount of fat deposited for a 3780 km migration is unknown, so the model was initiated with a body mass 50% >1.68 kg. We used 2 × RMR$_a$ as a nominal estimate of the cost of gliding flight (Baudinette and Schmidt-Nielsen 1974).

As in Smith et al.'s (1986) model, we assumed that fasting osprey engage in only two activities during migration, soaring flight (8 hr d^{-1}) and roosting (16 hr d^{-1}). A daily flight time of 8 hr was used as the nominal value in this model because this approximates the length of time convective fields used by migrating, soaring hawks are available in temperate latitudes (Kerlinger 1989). From this, daily fat consumed during roosting (RFC [kg d^{-1}]) can be calculated as:

$$RFC = (RMR_r \times T_r)/ e,$$

where T$_r$ is the daily roosting time in sec. In this equation, RMR$_r$ (Watts) is calculated from the unadjusted mass (1.68 kg) which is assumed to be a good approximation of lean body mass (M). The sum of FFC and RFC is the daily fat consumed (DFC [kg d^{-1}]).

The model was run iteratively, with DFC subtracted from initial body mass after each iteration (one day of migration). The program terminated when the new mass was <1.68 kg. Using the daily output, DDT, DFC and the number of iterations were individually summed from the termination point until the sum of DDT = 3780 km. The sums of DFC and the number of iterations were used as the predictions for total fat consumed and total migration time, respectively.

Sensitivity Analysis of the Fasting Model. We compared changes in predicted migration times and fat consumed under fasting conditions to uncertainties in the following model parameters: lean body mass, wingspan, wing area, wind speed, climb, altitude, daily flight time, total migration distance, RMR$_r$, and the energetic cost of gliding flight (Table 1). We were interested in discovering how robust the model predictions were to uncertainties inherent in these parameter estimates and thus, identify those parameters that must be carefully estimated empirically in future research.

Parameter uncertainties were estimated by assigning upper and lower parameter bounds and running the model separately varying one parameter at a time to its upper or lower bound (Table 1). The bounds for morphometric parameter values were based on ranges of measurements of western

Table 1. Results of the sensitivity analyses of all the parameters included in the fasting model for migrating osprey. Nominal and boundary values are presented.

PARAMETER (UNITS)	NOMINAL	RANGE	MIGRATION TIME (d)	FAT CONSUMED (g) (% FAT DENSITY)
Lean mass (kg)[a]	1.68	1.35–2.03	12–13	196(14)–293(14)
Wing area (m^2)[a]	0.30	0.24–0.33	12	239(14)–248(15)
Wing span (m)[a]	1.49	1.34–1.58	12	243(14)–247(15)
Altitude (m)[b]	2000	1000–3000	12	240(14)–249(15)
Climb (m s^{-1})[c]	3	2.5–3.5	11–13	225(13)–267(16)
Wind speed (m s^{-1})[d]	0	−5.0–+5.0	8–21	164(10)–447(27)
Flight time (hr d^{-1})[b]	8	6–10	10–16	205(12)–284(17)
Migration distance (km)[e]	3780	2940–4620	9–15	185(11)–304(18)
RMR (W)[f]	6.2	4.0–6.2	12	163(10)–247(15)
Cost of flight ($\times$RMR$_a$)[g]	2	2–4.5	12	247(15)–416(25)

[a] Nominal value from Kerlinger (1989) and bounds are from M. Bechard (unpubl. data).

[b] Estimated value (see text).

[c] Nominal value from Kerlinger et al. (1985 in Kerlinger 1989). Bounds were based on climb rates observed in other soaring hawks by Kerlinger et al. (1985 in Kerlinger 1989).

[d] Estimated value (see text). Positive values indicate a head wind and negative values indicate a tail wind.

[e] Nominal value is the mean of 21 band recovery distances from osprey breeding in the Intermountain West (Melquist et al. 1978, Melquist and Johnson 1984, Johnson and Melquist 1991). Upper and lower bounds are ±1 SD.

[f] Nominal value is the average resting metabolic rate (RMR) measured for three captive osprey during their resting phase (Wasser 1986) The lower bound is based on Wasser's allometric equation for estimating RMR for Falconiformes during their active phase. The nominal value was also used as the upper bound because these measurements are higher than predicted by any published allometric equation for estimating RMR for nonpasserines during their active phase.

[g] Values are based on Baudinette and Schmidt-Nielsen's (1974) measurements of energetic costs of gliding flight in herring gulls (*Larus argentatus*). The lower bound is based on the measured difference between resting metabolic rate and gliding metabolic rate in the wind tunnel. The upper bound is the difference between the measured gliding metabolic rate and the resting metablic rate calculated using Lasiewski and Dawson's (1967) equation for nonpasserines. The lower bound was used for the nominal value since metabolic rate during flight was calculated using active phase RMR.

osprey (M. Bechard unpubl. data). Bounds for the flight characteristics and wind speed were based on published variations of these parameters for migrating osprey or other large migrating raptors if data on osprey were not available (Kerlinger 1989, Kerlinger and Moore 1989). The nominal value for RMR$_r$ was used as its upper bound because Wasser's (1986) metabolic measurements on osprey were higher than the predictions from allometric equations. The lower bound for RMR$_r$ was estimated with Wasser's (1986) equation for resting phase RMR$_r$ in falconiformes. This equation predicts lower values for RMR$_r$ than do the equivalent allometric equations for nonpasserines (Aschoff and Pohl 1970, Lasiewski and Dawson 1967).

Foraging Migration Models. If these osprey chose not to fast during the entire migration, they would have to spend time foraging daily or break up their trip into several segments that are separated by stopovers to replenish their fat reserves. To compare fasting migration to foraging migration, the fasting model was modified to estimate total migration time and stopover fat deposition for jump or hop strategies (Piersma 1987). Migration models using the jump strategy included migrations with one stopover (after 1890 km) and three stopovers (one every 945 km), while the hop strategy included five stopovers (one every 630 km) and 11 stopovers (one every 315 km—the daily flight distance predicted by the foraging model).

To estimate fat-deposition rates at stopovers, maximum daily fat deposition rate (FDR$_{max}$) was calculated using Lindström's (1991) Eq. 1:

$$FDR_{max} = \frac{(DME_{max} - DEE_{min})}{M} \times \frac{(100\ n)}{E},$$

where FDR$_{max}$ is a percentage of lean body mass, DME$_{max}$ is maximum daily metabolizable energy intake in kJ, DEE$_{min}$ is minimum daily energy expenditure in kJ, M is lean body mass in kilograms, n is the conversion efficiency of metabolized energy into fat (0.88 [Kersten and Piersma 1987]), and E is the energy content of stored fat (3.96 $\times$ 10^4 kJ kg^{-1}). Like Lindström, DME$_{max}$ was calculated using Kirkwood's (1983) allometric equation; however we calculated DEE$_{min}$ as:

$$DEE_{min} = DEE + (DME_{max} \times 1\%), \quad \text{(Eq. 1)}$$

where DEE is the minimum daily energy expenditure of 1.5 BMR predicted by Lindström (1991). The additional term in Eq. 1 (DME$_{max}$ $\times$ 1%) estimates the additional energy expenditures incurred by hunting osprey (kJ d^{-1}) (Machmer and Ydenberg 1990).

Lindström and Alerstam (1992) observed that birds at stopover sites lose body mass during the first day at the site and/or there is a time lag before fat deposition starts, but Moore and Kerlinger (1987) found that weight gain can
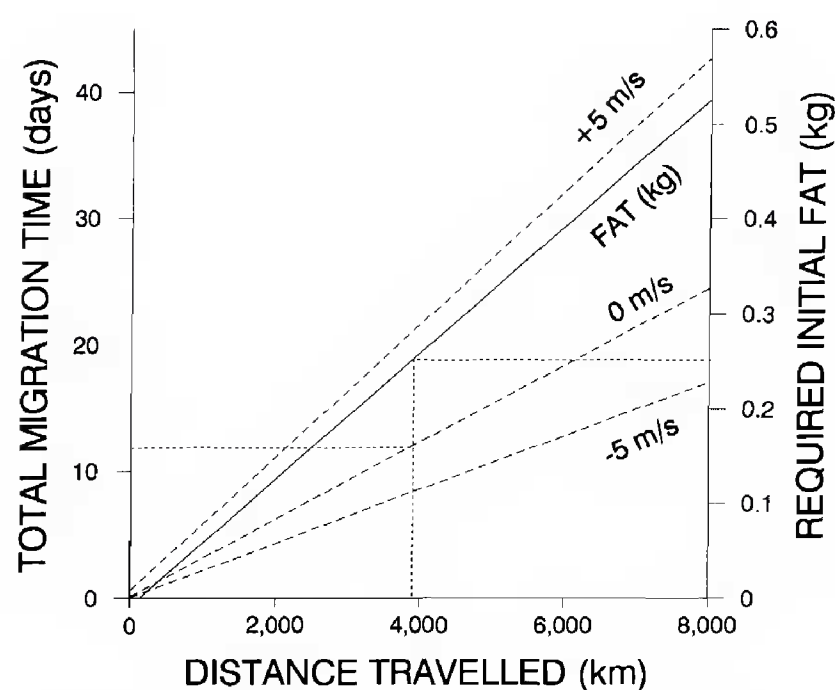
Figure 1. Fasting model predictions of total migration time at three different wind speeds (dashed lines) and required initial fat deposits (solid line) for an osprey breeding in the Intermountain West to complete a 3780 km southward migration. The dotted lines to the X and Y axes indicate the predicted duration and amount of premigratory fat deposition for migrations under nominal conditions.
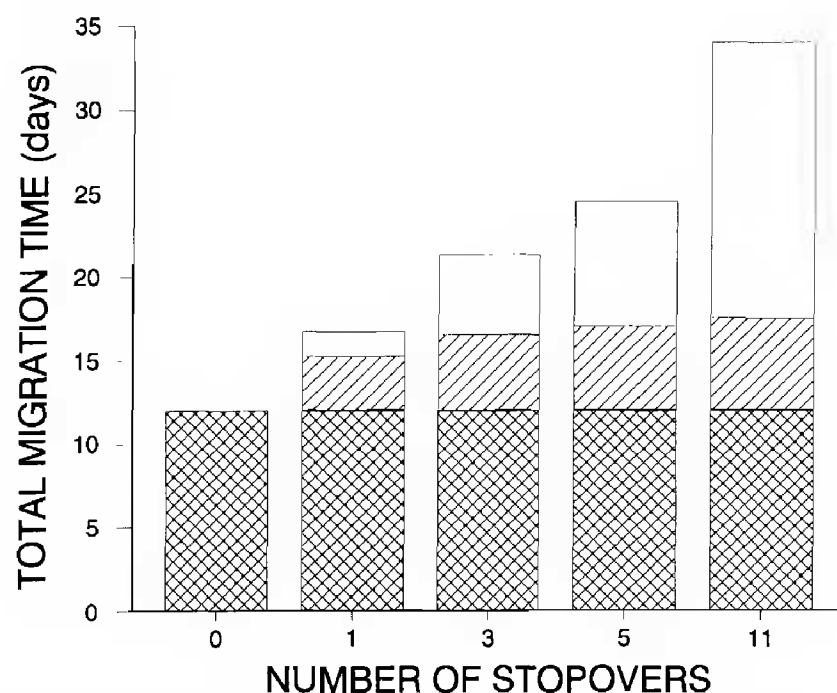

Figure 2. Foraging model predictions of total migration time with zero, one, three, five or 11 stopovers. The cross-hatched portion of each bar indicates the predicted time in flight, the hatched portion indicates the predicted total time foraging at stopovers, and the unshaded portion indicates the predicted total settling costs (time spent settling at stopovers [1 d stopover^{-1}] plus the extra time spent foraging to cover the energy expenditures of the days settling at stopovers). If there are no settling costs, then the total migration time is represented by the sum of the cross-hatched and hatched portions of the bar.

occur on their arrival day at a stopover. Therefore, we evaluated the foraging migration using three stopover strategies: (1) stopovers with one day of settling before weight gain begins; (2) stopovers with weight gain beginning on the first day of stopover; and (3) foraging daily without stopovers. In the first strategy we assumed (1) osprey's energy expenditures while settling were equal to DEE and (2) they arrived at stopovers with enough fat to spend one day without foraging.

RESULTS

Fasting-model Predictions. Fasting-model predictions are summarized in Fig. 1. The solid line in Fig. 1 represents model predictions for total fat consumption using nominal values listed in Table 1. Dashed lines are model predictions for distance traveled with the nominal value and the lower and upper bounds for wind speed. As indicated by the dotted lines in Fig. 1, we predict that a 1.68-kg osprey would take 12 d, consume 0.25 kg of fat (a fat density of 15% of lean body weight), to complete a fasting migration of 3780 km if it migrated with no head or tail wind.

Sensitivity Analysis of Fasting Model. The results of the sensitivity analysis of the fasting model are listed in Table 1. Variation in wind speed caused the greatest change in predicted fat consumption and migration time, with a 3780 km migration taking 21 d and 0.45 kg of fat (27% fat density) in a 5 m s^{-1} head wind, or 8 d and 0.16 kg of fat (10% fat density) in a 5 m s^{-1}

tail wind (Fig. 1). The amount of time a bird flies during the day and total distance migrated also resulted in large changes in model predictions. Flying 6 hr d^{-1} would increase migration time 33% and fat consumed 13%, while changing flight time to 10 h d^{-1} reduces the predicted migration time by 17% and fat consumed by 17%. An 840-km variation in migration distance changed migration time by 25% and fat consumed by 23–25%. Uncertainties associated with estimates of RMR and energetic cost of flight did not change the predicted migration time but did vary the predicted fat consumed by as much as 34% and 68%, respectively. Uncertainties associated with the other parameters caused predicted migration times to vary by no more than 1 d and predicted fat density to vary by only 1–2%.

Foraging-model Predictions. We estimate maximum daily fat deposition rate (FDR$_{max}$) to be 2.2% (0.04 kg d^{-1}) and that it would take 7 d of maximum energy intake to deposit a premigratory fat density of 15% of lean body mass (predicted fat density for a fasting migration of 3780 km). In comparison, based on Lindström's Eq. 1 (1991) and Lasiewski and Daw-

son's (1967) allometric Eq. E for estimating passerine BMR, a 0.015-kg passerine would require only 2 d of maximum energy intake to deposit a comparable premigratory fat density. Using Machmer and Ydenberg's (1990) estimates of 218 kJ average net energy gain per prey, an osprey would require 11 fish per d, or a total of 77 fish, to provide the fat stores required for a 3780 km fasting migration. The addition of stopovers to the migration would increase the predicted time investment to 15, 16, 17, and 18 d with one, three, five, and 11 stopovers, respectively (Fig. 2). However, if there is settling time at each stopover, the total migration time is predicted to increase to 17, 21, 25, and 34 d, respectively.

Model Evaluation. Although premigratory fat densities are not available for osprey, the predicted fat density of 15% is very close to the maximum fat density measured in comparably sized European goshawks (*Accipiter gentilis*) (16.4% in a 1.67-kg female, Marcström and Kenward 1980). This fat density prediction is also well below the premigratory fat densities that have been observed in warblers and waders (>50%, Blem 1980), and the predicted fat densities of migrating buteos (Smith et al. 1986). American kestrels (*Falco sparverius*) were found to have fall fat densities 2–4% higher than mid-summer values (5.3–7%, Gessaman 1979), but Kirkley and Jones (unpubl. data) point out that these fat levels are not maximal, and should be considered wintering fat since they are maintained throughout the winter. Obviously, more quantitative data on premigratory fat deposition in raptors will be necessary to determine if the fat deposition patterns predicted by this model occur in nature.

Based on the disappearance of resident birds from nesting territories, osprey migrations in northern Idaho begin as early as the first week of September (Melquist et al. 1978, Melquist and Johnson 1984). Peak numbers of osprey counted at a migration station in northern Utah occur during the second and third week of September (Hoffman 1990). Osprey from the Intermountain West are widespread in Mexico by late September (Melquist and Johnson 1984), with banded first-year migrants recovered in central Mexico as early as 17 September (2700 km from banding site [Melquist and Johnson 1984]) and adults recovered as early as 28 September even further south (4200 km from banding site [Melquist and Johnson 1984]). Osprey banded as nestlings from 14 July to 2 August were recovered 46–135 d later, after travelling a maximum of 3500 km from the banding site (Melquist and Johnson 1984). The predicted travel time of 12 d for a fasting migration

with no head wind is much less than the shortest times observed between banding and recovery, but may be comparable to actual migration times if osprey leaving Idaho in the beginning of September arrive in central Mexico by mid-September.

The model's prediction of 21 d for a fasting migration with a 5 m s^{-1} head wind is comparable to empirical estimates of migration times, but the predicted fat density of 27% is much higher than measured fat densities in raptors. These predictions suggest that osprey from the Intermountain West probably do not migrate entirely into head winds of this intensity. There are no observations of wind conditions along osprey migration routes in the Intermountain West to evaluate our conclusion. However, observations by Hall et al. (1992) demonstrate that significantly more coastal migrants in California migrate south with no wind or tail winds than with head winds.

The addition of five or more stopovers with settling costs increased the total migration time to 25–34 d (Fig. 2), which is 2–3 times the predicted migration time while fasting and slightly longer than the empirical migration time estimates based on band recoveries. With one or three stopovers, the predicted total migration time is 17 or 21 d, respectively (including settling costs). It seems unlikely that osprey would make frequent foraging stops that included a day of settling and a day of foraging. Settling times are mostly observed in territorial migrants that travel in large, intraspecific flocks (Lindström and Alerstam 1992). Because osprey migrate individually or in small flocks (Kerlinger 1989), it is possible they do not experience settling costs. Without settling costs the total migration time with multiple stopovers is predicted to be 15–18 d (Fig. 2).

Without these settling costs, frequent foraging throughout migration could occur with little affect on migration time if osprey foraged and flew in the same day. Although a 1.68-kg osprey may only be able to metabolize 11 fish d^{-1}, it may not take them a whole day to catch those fish. Osprey have one of the highest capture success rates of any raptor (Newton 1979). Swenson (1978) observed average fish catch rates for osprey to be 8.8–19.7 min fish^{-1}, and Machmer and Ydenberg (1990) observed an average of 10.3 min fish^{-1}. Therefore, with good forage availability, an osprey may require <2 hr to catch its metabolic maximum. Alternatively, osprey may only need about five fish d^{-1}, or 45–100 min of daily foraging, if their strategy is to cover the costs of a single migration day and not deposit fat for subsequent days. If there are

adequate water sources en route, e.g., reservoirs and lakes, it is possible that an osprey could forage daily without affecting its daily time in flight and total migration time by hunting at the beginning or end of each day before the thermals were strong enough for soaring.

CONCLUSIONS

Our foraging- (without settling costs) and fasting-model predictions are consistent with the limited data available on fall migration strategies of osprey breeding in the Intermountain West. Our results also suggest that, under certain assumptions, nonstop migration may be energetically possible for western interior osprey. Whether or not stopovers are used by these osprey is probably a function of the food availability en route. Hop strategies are generally thought to be the most favorable for conserving energy (Piersma 1987) but probably require plentiful food resources en route. In ecologically unfavorable situations, e.g., low food availability, fasting or jump strategies are more likely (Johnson and Herter 1990, Berthold 1993). Anecdotal observations of osprey carrying fish during migration (Kerlinger 1989) combined with few foraging areas in the semi-arid Southwest and Mexico would suggest a jump strategy as the best strategy for osprey migrating from the Intermountain West.

Although our predictions are consistent with empirical observations, our model was not evaluated rigorously because of the absence of observations on migration strategies of individual osprey. Programmable satellite transmitters are now available that are small enough (<30 g) for medium to large raptors, which allow investigators to measure migration and stopover times, and identify migration routes of individual birds (R.E. Ambrose, M.W. Britten, P. Howie and P.L. Kennedy unpubl. data). This new technology can also be used to measure the daily time in flight, a key parameter in our model. Based on our sensitivity analysis, precise estimates of wind speeds at the location of a bird in flight are also necessary for accurate predictions, but this type of information will probably not be available until anemometers can be attached to the satellite transmitters. Anemometers on osprey would measure airspeed moving past the bird (V_a) while the satellite transmitter would indicate changes in location, allowing the calculation of ground speed (V_g). $V_g - V_a$ could be used as an estimate of the wind velocity between migration locations.

Empirical data on premigratory and stopover fat deposition (if any) by migrating osprey are also needed to determine if this model adequately presents the major factors influencing fat deposition strategies. Total body electrical conductivity (TOBEC) has been used to estimate fat in live animals. However, a recent evaluation of this methodology by Skagen et al. (1993) indicates TOBEC accurately measures lean body mass but its lipid estimates have numerous potential errors. Other technologies are being evaluated to estimate lipids of free-ranging animals in a non-invasive manner (J.A. Gessaman pers. comm.). With these new technologies, osprey migration strategies can be determined empirically and these data can be used to evaluate the validity of our models.

LITERATURE CITED

ASCHOFF, J. AND H. POHL. 1970. Der Ruheumsatz von Vogeln als Funktion der Tageszeit und der Korpergrosse. *J. Ornithol.* 111:38–47.

ALERSTAM, T. 1990. Bird migration. Cambridge Univ. Press, Cambridge, U.K.

BAUDINETTE, R.V. AND K. SCHMIDT-NIELSEN. 1974. Energy cost of gliding flight in herring gulls. *Nature* 248: 83–84.

BAKER, R.R. 1982. Migration paths through time and space. Holmes and Meier Publishers, Inc., New York, NY U.S.A.

BERTHOLD, P. 1993. Bird migration. A general survey. Oxford Univ. Press, Oxford, U.K.

BLEM, C. 1980. The energetics of migration, pages 175–224 *in* S.A. Gauthreaux [ED.], Animal migration, orientation, and navigation. Academic Press, New York, NY U.S.A.

CASTRO, G. AND J.P. MYERS. 1989. Flight range estimates for shorebirds. *Auk* 106:474–476.

GESSAMAN, J.A. 1979. Pre-migratory fat in the American kestrel. *Wilson Bull.* 91:625–626.

GOLDSTEIN, D.L. AND N.G. SMITH. 1991. Response to Kirkley. *J. Raptor Res.* 25:87–88.

GUDMUNDSSON, G.A., Å. LINDSTRÖM, AND T. ALERSTAM. 1991. Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres. Ibis* 133:140–152.

HALL, L.S., A.M. FISH AND M.L. MORRISON. 1992. The influence of weather on hawk movements in coastal northern California. *Wilson Bull.* 104:447–461.

HENNY, C.J. AND W.T. VAN VELZER. 1972. Migration patterns and wintering localities of American osprey. *J. Wildl. Manage.* 36:1133–1138.

HOFFMAN, S.W. 1985. Raptor movements in inland west-

ern North America: a synthesis, pages 325–337 *in* M. Harwood [ED.], Proceedings of hawk migration conference IV. Hawk Migration Assoc. of North America, Medford, MA U.S.A.

———. 1990. Southwest region. *J. Hawk Migr.* 16:87–89.

JOHNSON, D.R. AND W.E. MELQUIST. 1991. Wintering distribution and dispersal of northern Idaho and eastern Washington ospreys. *J. Field Ornithol.* 62:517–520.

JOHNSON, S.R. AND D.R. HERTER. 1990. Bird migration in the arctic: a review. pages 22–43 *in* E. Gwinner [ED.], Bird migration: the physiology and ecophysiology. Springer-Verlag, Berlin, Germany.

KENNEDY, P.L. AND J.A. GESSAMAN. 1991. Diurnal resting metabolic rates of accipiters. *Wilson Bull.* 103:101–105.

KERLINGER, P. 1989. Flight strategies of migrating hawks. Univ. Chicago Press, Chicago, IL U.S.A.

——— AND F.R. MOORE. 1989. Atmospheric structure and avian migration. *Curr. Ornithol.* 6:109–142.

KERSTEN, M. AND T. PIERSMA. 1987. High levels of energy expenditure in shorebirds, metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175–187.

KIRKLEY, J.S. 1991. Do migrant Swainson's hawks fast *en route* to Argentina? *J. Raptor Res.* 25:82–86.

KIRKWOOD, J.K. 1983. A limit to metabolizable energy intake in mammals and birds. *Comp. Biochem. Physiol. A* 75:1–3.

LASIEWSKI, R.C. AND W.R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.

LINDSTRÖM, Å. 1991. Maximum fat deposition in migrating birds. *Ornis Scand.* 22:12–19.

——— AND T. ALERSTAM. 1992. Optimal fat loads in migrating birds: a test of the time-minimizing hypothesis. *Am. Nat.* 140:477–491.

——— AND T. PIERSMA. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* 135:70–78.

LUKE, A. AND D.A. SCHOELLER. 1992. Basal metabolic rate, fat-free mass, and body cell mass during energy restriction. *Metabolism* 41:450–456.

MACHMER, M.M. AND R.C. YDENBERG. 1990. Weather and osprey foraging energetics. *Can. J. Zool.* 68:40–43.

MARCSTRÖM, V. AND R. KENWARD. 1980. Sexual and seasonal variation in condition and survival of Swedish goshawks. *Ibis* 123:311–327.

MELQUIST, W.E. AND D.R. JOHNSON. 1984. Additional

comments on the migration of northern Idaho and eastern Washington ospreys. *J. Field Ornithol.* 55:483–485.

———, ——— AND W.D. CARRIER. 1978. Migration patterns of northern Idaho and eastern Washington ospreys. *Bird-Banding* 49:234–236.

MOORE, F. AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

ÖSTERLÖFF, S. 1977. Migration, wintering areas, and site tenacity of the European osprey *Pandion h. haliaetus* (L.). *Ornis Scand.* 8:61–78.

PENNYCUICK, C.J. 1989. Bird flight performance. A practical calculation manual. Oxford Univ. Press, Oxford, U.K.

PIERSMA, T. 1987. Hop, skip, or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. *Limosa* 60:185–194.

———. 1990. Pre-migratory "fattening" usually involves more than deposition of fat alone. *Ringing & Migr.* 11: 113–115.

POOLE, A.F. AND B. AGLER. 1987. Recoveries of ospreys banded in the United States, 1914–84. *J. Wildl. Manage.* 51:148–155.

ROBBINS, C.T. 1993. Wildlife feeding and nutrition. Academic Press Inc., San Diego, CA U.S.A.

SKAGEN, S.K., F.L. KNOPF AND B.S. CADE. 1993. Estimation of lipids and lean mass of migrating sandpipers. *Condor* 95:944–956.

SMITH, N.G., D.L. GOLDSTEIN AND G.A. BARTHOLOMEW. 1986. Is long-distance migration possible for soaring hawks using only stored fat? *Auk* 103:607–612.

SWENSON, J.E. 1978. Prey and foraging behavior of ospreys on Yellowstone Lake, Wyoming. *J. Wildl. Manage.* 42. 87–90.

WASSER, J.S. 1986. The relationship of energetics of falconiform birds to body mass and climate. *Condor* 88:57–62.

WELHAM, C.V.J. 1994. Flight speeds of migrating birds. a test of maximum range speed predictions from three aerodynamic equations. *Behav. Ecol.* 5:1–8.